

LEAF ANATOMY AND VENATION PATTERNS
OF THE STYRACACEAE¹

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THE STYRACACEAE is a woody, dicotyledonous family that is generally described as containing 12 or 13 genera and 150 to 190 species (Wood & Channell, 1960; Hutchinson, 1973; Gonsoulin, 1974; Spongberg, 1976). The plants are distributed primarily in eastern Asia to western Malaysia, tropical South America, and the southeastern United States. Ecologically, the plants occupy a variety of habitats.

The largest genus, *Styrax* L., includes about 120 species and is widely distributed in the tropical and warm temperate regions of eastern Asia and America. A conspicuous exception to this distribution pattern is *Styrax officinalis* L., which is found in the Mediterranean region and in California. In Asia the numerous species extend from the eastern Himalayas to Malaysia, Indochina, Korea, and Japan. The New World species are widely distributed from Pacific to Atlantic North America, the West Indies, southward to Venezuela and southern Brazil.

Two sections of the genus were recognized by Perkins (1907): STYRAX (*Eustyrax* Perk.), with the ovary 16- to 24-ovulate, and FOVEOLARIA (Ruiz & Pavon) Perk., with the ovary 3- to 5-ovulate. Section STYRAX was divided by Gürke (1891) and Perkins (1907) into two series, Valvatae and Imbricatae, on the basis of aestivation of the corolla lobes. As van Steenis (1932) has shown, however, imbrication varies widely with respect to both individual plants and species. The genus *Halesia* Ellis ex Linnaeus (about 5 species) occurs in southeastern North America and in eastern Asia, *Bruinsmia* Boerlage & Koorders (2 species) is found in Assam, Burma, and Malaysia (excluding the Malay Peninsula), *Pamphilia* Martius ex A. de Candolle (3 species) is located in Brazil, and *Afrostryax* Perkins & Gilg (2 species), which according to Baas (1972) is better placed in the family Huaceae of the Malvales, occurs in tropical Africa. The remainder of the genera are distributed from the Himalayas through China and Japan: *Alniphyllum* Matsumura (8 species), China and Formosa; *Pterostyrax* Siebold & Zuccarini (7 species), Burma to Japan; *Rehderodendron* Hu (10 species), China and Indochina; *Huodendron* Rehder (6 species), southern China, Siam, and Indochina; *Sinojackia* Hu (3 species), southern China; *Parastyrax* W. W. Smith (1 species), Burma; and *Melliodendron* Handel-Mazzetti (3 species), southern and southwestern China.

As reviewed by Spongberg (1976), the flowers of the Styracaceae are

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perfect and actinomorphic. Inflorescences are often reduced, and the flowers are usually arranged in simple or sometimes branched, terminal and/or axillary racemes, corymbs, or panicles and are sometimes solitary or in few-flowered fascicles. The calyx is often articulated at the base, synsepalous, tubular, subentire or 4- or 5-lobed (rarely more), often united into a tube only at the base. The insertion of the corolla is hypogynous to epigynous, and the lobes are valvate or imbricate in bud. The stamens are usually twice the number of the corolla lobes, sometimes more; epipetalous; inserted in 1 whorl on the base of the corolla (or rarely at the base of the ovary), with the filaments usually being connate into a tube below (free above) and the anthers being 4-locular. The gynoecium is syncarpous. The ovary is superior and completely free to inferior and completely adnate to the calyx tube and is 3- to 5-locular, often 1-locular above. Each locule has 1 to many ovules on axile placentae. Each flower has a single slender style terminated by a usually 3- to 5-lobed stigma. The fruits are dry, often woody, dehiscent or indehiscent capsules or drupes, and the seeds number from 1 to many. The embryo is usually straight with broad cotyledons and is embedded in a fleshy endosperm.

In the general systems of Bentham and Hooker (1876), Engler and Prantl (Perkins, 1907), Bessey (1915), Cronquist (1968), Thorne (1968, 1976), and Takhtajan (1969, 1973), there is general agreement on the placement of the Styracaceae in the Ebenales. This same treatment was followed by G. Wagenitz (1964) in the latest edition of Engler's *Syllabus der Pflanzenfamilien*. Hutchinson (1926, 1959, 1967, 1969, 1973), however, placed the family in the order Styracales, along with the families Lissocarpaceae and Symplocaceae. The families Ebenaceae, Sapotaceae, and Sarcospermataceae were considered to constitute the distinct order Ebenales. Hutchinson (*op. cit.*) derived the Styracales from the Rosales via the Cunoniales and derived the Ebenales (*sensu stricto*) from the Myrsinales. Huber (1963) suggested a relationship between Symplocaceae and Styracaceae and the Cornaceae, incorporating them in the order Cornales which he derived from the Cistiflorae, especially Theaceae. Airy Shaw (in Willis, 1973) denied affinities between Symplocaceae and Styracaceae. According to Airy Shaw (*op. cit.*), Styracaceae is related to Philadelphaceae (also placed in the Cornales by Huber), and Symplocaceae is related to Theaceae. Cronquist (1968), Thorne (1968, 1976), and Takhtajan (1969, 1973) were of the opinion that the Ebenales, including the families Sapotaceae, Ebenaceae, Symplocaceae, Styracaceae, and Lissocarpaceae, form a natural group and that the origin of the order lies among the thealean complex. According to Wood and Channell (1960), these 5 families are characterized by sympetalous corollas with stamens generally two to three times as many as the corolla lobes (or, by abortion, equal in number to and opposite them) and by superior to inferior, incompletely to completely loculed ovaries with axile placentation. Wagenitz (1964) concluded that the Ebenales should also include two additional families, Hoplestigmataceae and Sarcospermataceae. Dahlgren (1975) felt that only the families Styracaceae, Sapotaceae, Lissocarpaceae, and Ebenaceae comprised the

Ebenales and that the Symplocaceae was better placed in Theales. According to Nooteboom (1975), Symplocaceae does not belong in the Ebenales but shows more affinity to Cornaceae and possibly Theaceae on the basis of evidence derived from chromosome numbers, chemotaxonomy, anatomy (wood and leaf), germination studies, and a survey of morphological characters. Such arguments indicate that the order Ebenales (*sensu lato*), including the families Lissocarpaceae, Styracaceae, Ebenaceae, Sapotaceae, and Symplocaceae, may not be a very natural assemblage and is in need of redefinition.

The first comprehensive anatomical investigation of styracaceous leaves was the family treatment by Solereder (1908). Metcalfe and Chalk (1950) provided additional observations, but information regarding the leaf anatomy of this family is still very incomplete. Other literature containing general information about leaf characters includes work by Gürke (1891), Perkins (1907, 1928), Mori (1936), Mears (1972), Baas (1972), Fahn (1974), Gonsoulin (1974), Hickey and Wolfe (1975), and Sarcar and Banerji (1975).

The present research was undertaken to examine the leaf anatomy (including venation patterns) of the Styracaceae in order to provide additional evidence for generic circumscription and to shed additional light on the intrafamilial and interfamilial relationships of the family. The specific objectives of this initial investigation are: 1) to provide a comprehensive description of the leaf structure of the Styracaceae, 2) to outline basic trends of structural specialization in the anatomy and architecture of styracaceous leaves, and 3) to provide anatomical data that will eventually contribute to a better understanding of the intrafamilial and interfamilial systematics and relationships of the family.

MATERIALS AND METHODS

Leaves from all 12 genera recognized as comprising the family Styracaceae (*sensu* Hutchinson, 1973) were studied. Material of the related genus *Lissocarpa* (Lissocarpaceae, 2 species, tropical South America) was also examined. A total of 82 species were investigated (APPENDIX). Transverse sections of leaves were prepared according to standard procedures of paraffin embedding and sectioning (Johansen, 1940). Sections were taken from the central part of the lamina (including the midrib) and from the basal, medial, and distal portions of the petiole. Since almost all specimens were gathered from dried herbarium collections, it was necessary to reexpand the leaves initially in 5 percent NaOH before fixation in 70 percent FAA and dehydration. Transverse sections were stained with safranin and fast-green. Cleared leaves were prepared using the NaOH method outlined by Arnott (1959) and were subsequently stained with safranin. Using cleared leaves and temporary free-hand peels, stomatal patterns were observed. Ten stomata per specimen were measured at the widest part of the guard cell pair and from pole to pole. Averages and ranges for stomatal width and length were recorded. Drawings were made

using a Wild dissecting microscope with a drawing tube attachment. Photomicrographs of transverse sections and cleared preparations were made using a Zeiss photomicroscope.

For the description of leaf architecture, the terminology of Hickey (1973), with necessary additions and modifications, was followed. For the genus *Styrax* the masculine gender was implemented following the suggestion of Nicolson and Steyskal (1976).

Slides are deposited in the Department of Botany, The University of North Carolina at Chapel Hill, and in the Department of Botany, Smithsonian Institution, Washington, D. C.

OBSERVATIONS

SUMMARY OF LEAF ANATOMY OF THE STYRACACEAE (*sensu stricto*)

Petiole transverse section. Cuticle smooth or minutely furrowed. Epidermis uniseriate. Epidermal cells irregular to more or less rectangular to square in outline and with moderately thin walls. Parenchymatous cortex undifferentiated except in the monotypic genus *Parastyrax*, where outer half is collenchymatous and inner half parenchymatous. Crystals occurring as scattered druses, scattered prismatic crystals, a combination of druse and prismatic crystals, or, as in *Parastyrax*, crystal sand. Numerous solitary and clustered brachysclereids present in *Huodendron*.

Vasculature of petiole variable within the family. Five different vascular configurations occurring in basal portion of petiole: 1) arc, 2) arc with two dorsal cortical bundles, 3) arc with invaginated ends, 4) arc with invaginated ends and two dorsal collateral bundles, and 5) dissected cylinder of collateral bundles with numerous medullary bundles and four smaller dorsal dissected cylinders. At distal end of petiole, the following patterns occur:

- 1) Arc with invaginated ends: *Styrax americanus* var. *americanus* (PLATE III, C), *S. americanus* var. *pulverulentus*, *S. hypargyreus*, *S. paralleloneurus*.
- 2) Arc with invaginated ends accompanied by two dorsal cortical bundles: *Pamphilia aurea* (PLATE III, A), *P. pedicellata* var. *ovalis*, *P. styracifolia*, *Styrax argenteus* var. *argenteus*, *S. argenteus* var. *lintonii*, *S. argenteus* var. *ramirezii*, *S. benzoin* (PLATE IV, A), *S. camporum*, *S. formosanus*, *S. glaber*, *S. glabrescens* var. *glabrescens*, *S. glabrescens* var. *pilosus*, *S. grandifolius*, *S. henryi*, *S. hypoglaucus*, *S. japonicus* (PLATE III, D), *S. langkongensis*, *S. obtusifolius*, *S. officinalis* var. *fulvescens*, *S. officinalis* var. *redivivus*, *S. philadelphoides*, *S. platanifolius*, *S. portoricensis*, *S. subcrenatus*, *S. suberifolius*, *S. sumatranus*.
- 3) Medullated cylinder: *Halesia macgregorii*, *Huodendron biaristatum*, *H. chunianum*, *H. tibeticum*, *Sinojackia henryi*, *S. rehderiana*, *S. xylocarpa* (PLATE III, B), *Styrax agrestis*, *S. faberi*.

- 4) Medullated cylinder accompanied by two dorsal cortical bundles: *Alniphyllum eberhardtii*, *A. fortunei*, *A. hainanense*, *A. pterospermum*, *Halesia carolina*, *H. diptera* var. *diptera*, *H. diptera* var. *magniflora*, *Meliiodendron wangianum*, *M. xylocarpum*, *Pterostyrax cavaleriei*, *P. corymbosus*, *P. hispidus*, *Rehderodendron indochinense*, *R. kweichowense* (PLATE II, B), *R. macrocarpum*, *Styrax ochraceus* (PLATE IV, C), *S. serrulatus*.
- 5) Medullated cylinder accompanied by medullary vascular tissue and two dorsal cortical bundles: *Bruinsmia styracoides*, *Styrax ambiguus*, *S. cespedesii*, *S. conterminus*, *S. crotonoides*, *S. davillifolius*, *S. fanshawei*, *S. ferrugineus*, *S. glabratus*, *S. heteroclitus*, *S. jaliscanus*, *S. latifolius*, *S. longifolius*, *S. macrocalyx*, *S. macrotrichus*, *S. martii*, *S. micrasterus* (PLATE IV, B), *S. microphyllus*, *S. ovatus*, *S. pallidus*, *S. pearcei*, *S. pentlandianus*, *S. pohlii* (PLATE IV, D), *S. poissonianus*, *S. pseudargyrophyllus*, *S. subcordatus*, *S. yapobodensis*.
- 6) Dissected cylinder of collateral bundles with numerous medullary bundles and two smaller dorsal dissected cylinders: *Parastyrax lacei* (PLATE II, A).

All cortical bundles in the family collateral except in *Styrax argenteus*, *S. davillifolius*, and *S. pohlii* (PLATE IV, D), where amphicribal bundles occur. Perivascular sclerenchymatous elements present distally. As vascular tissue enters lamina, configuration remains same as in distal portion of petiole for all species investigated except *Pamphilia* (PLATE III, A) and *Parastyrax* (PLATE II, A).

Petiole and lamina surface view. Trichomes present in all species investigated except *Halesia macgregorii*. They generally occur on petiole, as well as on both surfaces of lamina, in four combinations of structural types: 1) stellate only, 2) peltate only, 3) stellate and peltate, and 4) stellate and simple cylindrical. Cuticle smooth or striated. Within individual cells striations oriented in a single direction parallel to one another and sometimes continuous from cell to cell. Lamina epidermal cells of both surfaces varying in shape from irregular to more or less quadrangular to polygonal. Epidermal anticlinal cell walls moderately thin except in *Styrax argenteus*, *S. camporum*, *S. heteroclitus*, and *S. macrotrichus*, where moderately thick walls occur. Anticlinal cell walls of adaxial epidermis generally straight to slightly curved, being slightly sinuous to curved only in *Huodendron biaristatum*, *H. chunianum*, *Styrax glabrescens*, and *S. serrulatus*. Anticlinal cell walls of abaxial epidermis straight to slightly curved, slightly sinuous to curved, or sinuous. For all species investigated, stomata anomocytic, occurring only on abaxial surface, and ranging in mean width between 11 and 22 μm . and in mean length between 14 and 30 μm .

Venation pinnate, with the single midvein following a straight, unbranched course. Midvein of moderate size (1.25–2.00 percent) except

in *Sinojackia* (PLATE VI, E) and *Styrax platanifolius*, where it is thin (less than 1.25 percent). Midvein ensheathed by sclerenchymatous elements elongate along long axis. In *Parastyrax* (PLATE VI, B) venation actinodromous with a pair of lateral primary veins occurring on either side of a third, centrally located primary vein. The imperfectly developed, reticulate actinodromous lateral veins becoming attenuate exmedially and with secondary veins originating exmedially. In all pinnately veined species, secondary venation weakly cladodromous, eucamptodromous, or transitional from eucamptodromous basally to brochidodromous distally. In species that are brochidodromous distally, loop-forming branches of secondaries join superjacent secondaries at right and acute angles. Relative thickness of secondary veins moderate, and their course branched when cladodromous, uniformly curved when eucamptodromous, and abruptly curved when brochidodromous. Exmedially, they are attenuate except for brochidodromous veins, which are of uniform thickness, and are braced in all species by a system of tertiary and quaternary veins. Simple intersecondary veins occurring in all species investigated except *Halesia macgregorii* (PLATE V, G), *Rehderodendron* (PLATE VI, D), *Sinojackia* (PLATE VI, E), *Styrax conterminus*, *S. martii*, *S. officinalis* (PLATE VI, I), *S. subcordatus*, *S. subcrenatus*, *S. suberifolius*, and *S. yapobodensis*, in which intersecondary veins are composite. Intramarginal veins absent in all species. Tertiary veins originating from secondary veins at acute, right, and obtuse angles, their pattern varying within the family from percurrent to random reticulate. Percurrent tertiary veins simple to forked and close in all species in which they occur, except in the specimen of *Parastyrax* examined, where they are both closely and distantly arranged. Predominantly opposite percurrent tertiary veins have a constant oblique tertiary angle in *Parastyrax*, *Styrax argenteus* (PLATE VI, G), and *Styrax benzoin*, and an apically decreasing oblique tertiary angle in *Alniphyllum eberhardtii* (PLATE V, C), *Pterostyrax* (PLATE VI, C), and *Styrax jalisscanus*. Predominantly alternate percurrent tertiary veins have a constant oblique tertiary angle with the midvein in *Styrax cespidesii* and *Styrax macrotrichus*, and an apically decreasing oblique tertiary angle in *Alniphyllum fortunei*, *A. hainanense*, *A. pterospermum* (PLATE V, D), *Styrax crotonoides*, *S. heteroclitus*, and *S. latifolius*. In other species, tertiary veins percurrent only in basal portion of leaf and forming random reticulate patterns distally. Predominantly opposite percurrent tertiary veins occurring only in a basal position in *Huodendron chunianum*, *Styrax conterminus*, *S. ovatus*, *S. paralleloneurus*, and *S. yapobodensis*; predominantly alternate percurrent tertiary veins, only in a basal position in *Melliodendron* (PLATE V, I), *S. ambiguus*, *S. ferrugineus*, *S. glabrescens*, *S. henryi*, *S. hypoglaucus*, *S. langkongensis*, *S. longifolius*, *S. macrocalyx*, *S. martii*, *S. pentlandianus*, *S. poissonianus*, *S. pseudargyrophyllus*, *S. serrulatus*, *S. subcordatus*, *S. suberifolius*, and *S. sumatranus*. In all other cases, tertiaries form random reticulate patterns throughout leaf. Resolution of higher vein orders distinct. Quaternary and quinary veins follow a relatively random course, having bundle sheaths of either parenchymatous or

sclerenchymatous elements elongate along their long axes. Bundle sheaths predominantly sclerenchymatous, with parenchymatous sheathing occurring only in *Alniphyllum*, *Bruinsmia*, *Parastyrax*, *Styrax americanus*, *S. argenteus*, and *S. platanifolius*. Ultimate veinlets simple to branched, linear to curved, generally with weak bundle sheaths composed of elements similar to sheathing of their respective higher vein orders. Sheathing absent on ultimate veinlets in *Alniphyllum*, *Bruinsmia*, *Halesia* (except *H. macgregorii*, where present), *Melliodendron*, *Parastyrax*, and *Pterostyrax*. Marginal ultimate venation either incomplete or looped. Areoles irregular to quadrangular to polygonal in shape (PLATE VII, A–F). They are small (less than 0.3 mm.) in *Styrax crotonoides*, *S. pseudargyrophyllus*, and *S. suberifolius*; small and medium (0.3–1.0 mm.) in *Parastyrax*, *Styrax paralleloneurus*, and *S. sumatranus*; large (1.0–2.0 mm.) in *Styrax japonicus*; both medium and large in *Bruinsmia*; and medium in all other species investigated. Areolation imperfectly or well developed, being incomplete only in the specimens of *Styrax japonicus* examined. Areoles relatively randomly arranged except in *Huodendron biaristatum*, *H. chunianum*, *Sinojackia*, *Styrax crotonoides*, *S. pseudargyrophyllus*, *S. subcrenatus*, and *S. suberifolius*, where well developed and relatively highly oriented.

Minute, crenulate teeth present in some species investigated are vascularized by a tertiary vein that is slightly expanded at base of tooth and tapered near apex (PLATE VIII, A–D). A glandlike cap composed of thin-walled cells occurring at apex of each tooth. Such glandlike structures also occurring on the entire margins of *Styrax glabrescens*. Scattered circular glands, consisting of five to eight small, flattened cells surrounding a centrally depressed area, occurring on lower leaf surface of a few species of *Styrax*.

Lamina transverse section. Cuticle thicker on adaxial surface than on abaxial in about half of species investigated, and of equal thickness on both surfaces for other species. For all species adaxial cuticular thickness ranging from less than 1 μm . to 24 μm .; abaxial cuticular thickness, from less than 1 μm . to 4 μm . Epidermal cells of both surfaces thin-walled and irregular to more or less rectangular to square. Epidermis uniseriate except in *Styrax macrotrichus* (PLATE X, A), *S. micrasterus* (PLATE X, B), *S. portoricensis* (PLATE X, E), and *S. pseudargyrophyllus* (PLATE X, F), where biseriate epidermis (hypodermis?) is present. Abaxial epidermal cells smaller than adaxial cells. Anomocytic stomata level with or slightly raised above abaxial surface. All major veins raised above abaxial leaf surface.

Bifacial mesophyll composed of 1 or 2 layers of slightly to very elongate palisade parenchyma cells in all species except *Styrax ochraceus* (PLATE X, C), which has 2 or 3 distinct layers of palisade cells, and *Styrax macrotrichus* (PLATE X, A), *S. poissonianus*, and *S. portoricensis* (PLATE X, E), with only a weakly differentiated mesophyll of irregular to more or less rectangular parenchyma cells. Spongy tissue very compact, moderately

compact, or loose, generally consisting of more or less isodiametric to slightly lobed parenchyma cells. Secondary and tertiary veins with sclerenchymatous bundle sheaths composed of elements elongate along their long axes. Bundle sheath extensions present in some species, occurring in two patterns of positions, adaxial only, and adaxial and abaxial. They are composed of sclerenchymatous elements elongate along long axis of veins. In *Pamphilia aurea* Martius (PLATE IX, D) (Irwin *et al.* 20974 and 29208) some elements of bundle sheath extensions also elongate perpendicular to long axis of veins. Quaternary and quinary veins with predominantly sclerenchymatous sheaths (occurring only in *Alniphyllum*, *Bruinsmia*, *Parastyrax*, *Styrax americanus*, *S. argenteus*, and *S. platani-folius*) and generally lacking bundle sheath extensions. Crystals present in all plants investigated, occurring as scattered druses, scattered prismatic crystals, a combination of druse and prismatic crystals, or, as in *Parastyrax*, crystal sand. They are sometimes confined to cortical parenchyma of midrib and to parenchyma cells adjacent to veins. Vasculature of midrib variable within the family, consisting of an arc, usually with invaginated ends, a medullated cylinder, or a medullated cylinder with medullary vascular tissue. Midrib with perivascular sclerenchymatous elements in all species investigated except *Styrax americanus*. In *Parastyrax* the central actinodromous vein has a ring of collateral bundles surrounding a single collateral bundle. All collateral bundles have thin-walled sclerenchymatous caps.

Lissocarpa Bentham

(Lissocarpaceae, *sensu* Engler & Gilg, 1924)

Petiole transverse section. Cuticle smooth, epidermis uniseriate. Epidermal cells irregular in outline and with moderately thick walls. Parenchymatous cortex undifferentiated, containing prismatic crystals and numerous diffuse vesiculose sclereids (*sensu* Rao & Bhupal, 1973) irregular in outline. Basally, vascular tissue consists of an arc with invaginated ends accompanied by two dorsal collateral bundles (PLATE I, B). Medially, each invaginated end of the arc begins to fold back upon itself dorsally. Distally, dorsal folding of each invaginated end of the arc increases. Perivascular sclerenchymatous elements present both singly and in clusters. As vascular tissue of petiole enters lamina, products of dorsal folding separate from arc and subsequently fuse, forming a dorsal plate. Ends of arc also fuse, forming a medullated vascular cylinder.

Petiole and lamina surface view. Surface of petiole and lamina glabrous. Cuticle smooth. Adaxial epidermal cells of lamina irregularly shaped with moderately thick, extremely sinuous anticlinal walls. Abaxial epidermal cells resembling cells of upper surface. Diffuse vesiculose sclereids with numerous simple pits occurring singly and in clusters throughout mesophyll and in random association with vascular tissue. For the genus, stomata anomocytic, occurring only on abaxial surface, ranging in mean width between 28 and 29 μm ., and in mean length between 34 and 38 μm .

Venation pinnate, with single midvein following a straight, unbranched course. Midvein of moderate size (1.25–2.00 percent) and ensheathed by thick-walled sclerenchymatous elements. Secondary venation weakly brochidodromous and ensheathed by thick-walled sclerenchymatous elements elongate along long axis of veins. Acute angle of divergence, nearly uniform for all secondaries, is wide. Secondary veins relatively slender, their course abruptly curved; loop-forming branches of secondaries joining superjacent secondaries at right and acute angles and braced exmedially by system of tertiary and quaternary veins. Composite intersecondary veins present, but intramarginal veins absent. Tertiary veins originate from secondaries at acute, right, and obtuse angles, forming random reticulate pattern. They are ensheathed by moderately thick-walled sclerenchymatous elements elongate along long axis of veins. Resolution of higher vein orders not distinct. They consist of a ramified network terminating in numerous branched ultimate veinlets. Higher vein orders and ultimate veinlets ensheathed by thin-walled, irregular to rectangular sclerenchymatous elements elongate along their long axes. Marginal ultimate venation fimbriate. Imperfectly developed, randomly arranged areoles irregularly shaped and large (1.0–2.0 mm.). Teeth and glands absent.

Lamina transverse section. Cuticle thicker adaxially (5–6 $\mu\text{m}.$) than abaxially (3–4 $\mu\text{m}.$). Epidermis uniseriate. Epidermal cells of adaxial surface thin-walled and irregular to more or less rectangular in outline; those of both surfaces approximately equal in size. Anomocytic stomata level with abaxial leaf surface. All major veins raised above abaxial leaf surface.

Bifacial mesophyll with 1 or 2 layers of short, more or less rectangular palisade parenchyma cells and several layers of fairly loose spongy tissue of isodiametric to slightly lobed cells. Sclerenchymatous bundle sheaths without bundle sheath extensions are conspicuous around all orders of venation. Prismatic crystals confined to parenchyma cells adjacent to veins. Diffuse vesiculose sclereids, irregularly shaped in outline, occurring in mesophyll. Midrib with medullated vascular cylinder accompanied by dorsal plate. Perivascular sclerenchymatous elements present.

Afrostryax Perkins & Gilg

Petiole transverse section. Cuticle smooth, epidermis uniseriate. Epidermal cells square to rectangular in outline and with moderately thin walls. Parenchymatous cortex undifferentiated except in one specimen of *Afrostryax kamerunensis* (Mildbraed 10688 (A)), where small amount of periderm and 2 or 3 layers of collenchyma observed in outer portion of cortex. Cortex containing prismatic crystals. Basally and medially, vascular tissue of petiole consisting of two large, C-shaped vascular bundles and one smaller, abaxially positioned one (PLATE I, A). Distally, the two large, C-shaped lateral bundles invaginate at the dorsal ends. Perivascular sclerenchymatous elements present. As vascular tissue of petiole

enters lamina, invaginated dorsal ends of C-shaped lateral bundles separate from lateral bundles, subsequently becoming medullary bundles. The two lateral C-shaped bundles fuse dorsally, enclosing the medullary bundles, which vary in number from one to several depending on whether invaginated portions fuse or divide. Baas (1972) reports *A. lepidophyllus* as having a more complex vascularization than *A. kamerunensis* as the result of a larger, although variable, number of medullary bundles present.

Petiole and lamina surface view. Stellate trichomes occurring infrequently on petiole and lamina of both species. Numerous peltate scales and short, uniseriate, two- to three-cellular trichomes occurring on petiole and lamina surfaces of *Afrostryrax lepidophyllus* but lacking on *A. kamerunensis*. Cuticle smooth. *Afrostryrax lepidophyllus* with adaxial epidermal cells of lamina quadrangular to polygonal, and having thin, slightly sinuous to curved anticlinal walls; *A. kamerunensis*, however, with anticlinal epidermal walls very sinuous. With exception of cells underlying major veins and resembling cells of adaxial surface, abaxial epidermis of *A. lepidophyllus* almost completely composed of dome-shaped papillate cells. This condition absent in *A. kamerunensis*, where abaxial epidermal cells smaller but otherwise identical to upper surface cells (which have very sinuous anticlinal walls). For the genus, stomata paracytic with crescent-shaped subsidiary cells, occurring only on abaxial surface. Mean stomatal width 11 μm .; mean length ranging between 15 and 16 μm .

Venation pinnate, with single midvein following a straight, unbranched course (PLATE V, A). Midvein of moderate size (1.25–2.00 percent) ensheathed by moderately thick-walled sclerenchymatous elements elongate along long axis of midvein. Secondary venation transitional from eucamptodromous basally to brochidodromous distally, also ensheathed by moderately thick-walled sclerenchymatous elements elongate along long axis of veins. Acute angle of divergence, nearly uniform for all secondaries, moderate. Relative thickness of the secondary veins moderate, their course uniformly curved. Exmedially, secondary veins are attenuate and braced by system of tertiary and quaternary veins. Intersecondary and intramarginal veins absent. Tertiary veins originating from secondaries at approximately right angles and forming orthogonal reticulate patterns with other tertiaries. They have a sheath of thin-walled parenchymatous cells slightly elongate along long axis of veins. Resolution of higher vein orders distinct. Both quaternary and quinary veins following an orthogonal course and having weak, incomplete parenchymatous sheaths. The few ultimate veinlets simple, linear to curved, without sheathing. Marginal ultimate venation fimbriate. The well-developed, oriented areoles quadrangular and small (less than 0.3 mm.) (PLATE VII, A). Teeth absent, but oval-shaped glands composed of elongate, thin-walled cells present on lamina margins.

Lamina transverse section. Cuticle smooth and of equal thickness (less than 1 μm .) on both surfaces. Epidermis uniseriate. Epidermal cells of adaxial surface thin-walled and square to rectangular in outline.

Cells of abaxial surface smaller than adaxial cells. Majority of abaxial cells of *Afrostryax lepidophyllus* papillate with an outer dome-shaped configuration (PLATE IX, A), a condition absent in *A. kamerunensis*. Paracytic stomata slightly raised above level of abaxial leaf surface. All major veins raised above level of abaxial leaf surface.

Bifacial mesophyll with 1 or 2 layers of elongate palisade parenchyma cells and two to several layers of moderately compact spongy tissue of more or less isodiametric to slightly lobed cells. Sclerenchymatous elements ensheathing secondary veins and forming adaxial and abaxial caps exterior to parenchymatous bundle sheaths of tertiaries. Both secondary and tertiary veins with conspicuous parenchymatous adaxial and abaxial bundle sheath extensions. Quaternary and quinary veins with weak, incomplete parenchymatous sheaths and parenchymatous adaxial and abaxial bundle sheath extensions. Prismatic crystals occurring in parenchyma cells adjacent to veins and in cortical region of midrib. Midrib with medullated vascular cylinder having variable number of medullary bundles. Perivascular sclerenchymatous elements present.

DISCUSSION AND CONCLUSIONS

Leaves of Styracaceae are considerably more variable morphologically and anatomically than previous descriptions indicate. Characters that are present in leaves of nearly all species investigated include bifacial mesophyll, anomocytic stomata confined to the abaxial surface, crystals in the form of druse and/or prismatic shapes, trichomes of the stellate, peltate, or simple cylindrical type, sheathing and supporting elements associated with the venation, and pinnate primary venation accompanied by camptodromous secondary venation.

Interestingly, almost all variation observed in the leaf structure of the ten smaller styracaceous genera is encountered among species of the large genus *Styrax*. Leaf characters that are not present in *Styrax* but which occur elsewhere in the Styracaceae include the distinct petiolar brachysclereids in *Huodendron*, the sclerenchymatous supporting sheath cells in *Pamphilia aurea* Martius (Irwin *et al.* 20074 and 20208) that are perpendicular to the long axis of the veins, and the unique features of crystal sand, actinodromous venation, and petiole vasculature in *Parastyrax*. Although many foliar characters appear to be extremely useful in the delimitation of taxa, a larger sample size is needed to confirm these observations.

Some of the anatomical variation lends itself to possible ecological interpretation, although the absence of detailed habitat data for many of the specimens observed makes such interpretation difficult. In coriaceous leaves, such as those of Brazilian *Pamphilia*, there does appear to be a strong correlation between more intensive sclerification along the veins and veinlets, the presence of inrolled leaf margins, thicker cuticles on both surfaces, compact spongy mesophyll, and an extremely dense indumentum on the abaxial surface of the leaves. Many of these characters have been

associated in other families with adaptations to a dry environment and may represent similar adaptation by styracaceous species. In leaves of species typically found in a mesic environment, such as *Halesia* (which occurs naturally in southeastern U. S. and China), there appears to be a strong correlation between less sclerification along the veins and veinlets, thinner cuticles on both surfaces, abundant air spaces in the spongy mesophyll, and less dense indumentum.

Relative levels of specialization of the foliar venation of woody dicots have been determined through comparative morphological studies of fossil and extant leaves (Hickey, 1971; Hickey & Doyle, 1972; Hickey, 1973; Hickey & Wolfe, 1975; Hickey & Doyle, 1977). Trends of specialization are represented by: 1) an increase in regularity of both low and high order venation; 2) a shift from indistinct vein orders to vein orders that are readily distinguishable from one another; 3) a shift from tertiary veins that follow a random course to tertiary veins that are very regular, often with rigid percurrent veins traversing the intercostal areas; and 4) a progressive development from random, incomplete areolation to orthogonal, well-developed (perfect) areolation. The venation of the Styracaceae is predominantly at an advanced level of organization in accordance with the above trends. The secondary veins are generally regular in course, and the tertiary veins linking the secondaries demonstrate trends toward being numerous, well differentiated, percurrent, and regularly spaced in a close arrangement. Another index of advancement is the formation of well-developed areoles of relatively constant size and placement in which veinlets are either absent or short and unbranched as in *Huodendron*, *Parastyrax*, *Sinojackia*, and several species of *Styrax*.

Petiole vasculature of the Styracaceae is quite diverse and, with the exception of that found in *Parastyrax*, consists of an arc, an arc with invaginated ends, a medullated cylinder, or a medullated cylinder with medullary tissue; these characters may or may not be accompanied by cortical bundles. In the leaves of several species of *Styrax*, the occurrence of both medullary and cortical petiolar vasculature is correlated with compact spongy mesophyll and an increase in leaf coriaceousness. Whereas each of the styracaceous genera except *Styrax* is characterized by a single vascular configuration, all observed patterns of petiole vasculature occur among species of the large genus *Styrax*. The presence in the petiole of *Parastyrax* of a highly dissected cylinder of collateral bundles that is accompanied by numerous medullary bundles and two smaller dorsal dissected cylinders is exceptional for the family.

Minute, crenulate teeth are present in all genera investigated except *Huodendron* and *Pamphilia*. Each tooth is vascularized by a medial vein that is usually slightly expanded at the base and tapered near the apex. A glandlike cap composed of thin-walled cells occurs at the apex of each tooth. Hickey and Wolfe (1975) described what they termed the "Theoid Tooth and its inferred variants" as present in the Ebenales, but it is not certain whether the typical styracaceous tooth morphology observed in this study falls within the limits of variation observed in that survey.

Although trichomes have traditionally been employed for systematic purposes in the Styracaceae (Perkins, 1907; Standley & Steyermark, 1940; Gonsoulin, 1974), it is clear that their morphological diversity has not yet been satisfactorily described. Among stellate trichomes, enormous variation within the family can be observed in such features as size, color, distribution, mode of attachment, appressed as opposed to stalked habit, number of arms, thickness of arms, degree of lateral fusion of arms, and number and orientation of cells composing each arm. Because of the large amount of gradation between these features, the value of stellate trichomes as diagnostic characters for separating taxa within the family is uncertain until these trichomes are more accurately characterized by employing a wider range of materials. The same difficulties are also evident, although to a much lesser extent, among peltate scales and simple cylindrical trichomes.

Baas (1972) presented evidence for the removal of *Afrostryrax* from the Styracaceae and for its subsequent placement in the malvacean family Huaceae. The present study affirms these conclusions. The number of characters separating the Huaceae from the Styracaceae is substantial. Characters distinguishing *Afrostryrax* leaves from styracaceous foliage include paracytic stomata, extremely well-developed, rectangular areolae, the presence of caducous stipules, and fimbriate marginal ultimate venation. According to Baas (1972), additional features distinguishing the Huaceae from the Styracaceae include the choripetalous corolla (vs. sympetalous in the Styracaceae), the 3-porate pollen (vs. 3-colporate), the trilacunar nodes (vs. unilacunar), and the cork arising in subepidermis (vs. in pericycle). The genus *Lissocarpa* was removed from the Styracaceae by Perkins (1907) and has subsequently been regarded as constituting the closely related monogeneric family Lissocarpaceae (*sensu* Engler & Gilg, 1924; Hutchinson, 1926, 1959, 1967, 1969, 1973). In addition to reproductive characters, features of foliar anatomy that can be used to separate *Lissocarpa* from the Styracaceae include diffuse vesiculose sclereids in the petiole and mesophyll, petiole vasculature consisting of an arc with outwardly curving ends, and fimbriate marginal ultimate venation.

The genus *Parastyrax* has a number of typical styracaceous floral characteristics (bisexual flowers axillary on new shoots; calyx subentire; petals 5, imbricate; stamens 10; anthers introrse; ovary usually inferior) but also has some leaf characters that are markedly different from the other styracaceous genera. These unique leaf characters include a distinctive petiolar vasculature, actinodromous primary venation, and the presence of crystal sand in the leaf mesophyll. Additional points of difference between *Parastyrax* and other taxa of the Styracaceae include its unusual height of 150 feet or more and its drupaceous fruit with a glabrous, fleshy exocarp marked with elongate, whitish lenticels (Smith, 1920). These distinguishing characters indicate that further intensive investigation of *Parastyrax* is warranted to discern more accurately its affinities with other styracaceous genera.

According to Wood and Channell (1960), the genus *Halesia* is most

closely related to *Pterostyrax*, *Rehderodendron*, *Sinojackia*, and *Melliodendron*. These five genera share a number of similar reproductive characters (including ovary two-thirds to completely inferior, four to eight ovules in each loculus, a single elongate style, and indehiscent fruit), as well as a substantial number of common leaf characters. According to Gonsoulin (1974), the genera *Alniphyllum* and *Pterostyrax* are most closely related to *Styrax*. *Alniphyllum* differs from *Styrax* mainly in its winged seeds and filaments connate distally to form a tube, whereas *Pterostyrax* differs from that genus primarily in its two-thirds to completely inferior ovary. These three genera share such reproductive characters as bisexual flowers, campanulate calyx, five corolla segments or free petals, ten stamens, and linear anthers. While it is true that there is a high correlation between the leaf characters of *Alniphyllum* and *Pterostyrax* and those of several species of *Styrax*, it is also true that almost all of the variation observed in the leaf characters of the ten small genera occurs in the large genus *Styrax*.

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APPENDIX. Specimens examined.

Afrostryax kamerunensis Perk. & Gilg. Cameroons: *J. Mildbraed* 10688 (A*); *G. Zenker* 3922 (US). *A lepidophyllus* Mildbraed. Congo: *G. Gilbert* 10222 (A), *J. Louis* 3965 (US).

Alniphyllum eberhardtii Guillaumin. Indochina: *A. Petelot* 4490 (US); *E. Poilane* 19043 (A). *A. fortunei* Perk. Chimen, China: *R. C. Ching* 3105 (A). *A. hainanense* Hay. Hainan, China: *C. I. Lei* 442 (US). *A. pterospermum* Matsum. Formosa: *E. H. Wilson* 9992 (US); label information illegible (US #1597269).

Bruinsmia styracoides Boerl. & Koord. New Guinea: *M. S. Clemens* 2970 (A). North Borneo: *J. & M. S. Clemens* 50339 (US).

Halesia carolina L. Jackson Co., North Carolina: *G. Nesom* s.n. (NCU). South Carolina: *H. D. House* 1866 (US). *H. diptera* var. *diptera* Ellis. Jefferson Co.,

* Herbarium abbreviations follow Holmgren and Keuken (1974).

Mississippi: *W. B. McDougall* 1430 (US). *H. diptera* Ellis var. *magniflora* Godfrey. Tallahassee, Florida: *R. K. Godfrey* 71367 (US). *H. macgregorii* Chun. Chekiang, China: *Ching* 2132 (US).

Huodendron biaristatum (W. W. Smith) Rehder. Indochina: *Petelot* 6339 (US). *H. chunianum* Hu. Yunnan, China: *H. T. Tsai* 60571 (A). *H. tibeticum* (Anthony) Rehder. Tibet: *J. F. Rock* 22020 (US).

Lissocarpa benthamii Gürke. British Guiana: *H. A. Gleason* 724 (GH). *L. guianensis* Gleason. British Guiana: *J. S. de la Cruz* 3076 (GH); *N. Y. Sandwith* 1590 (US).

Melliodendron wangianum Hu. Szechwan, China: *Chiao & Fan* 364 (A). *M. xylocarpum* Handel-Mazz. Kwangsi-Chuang, China: *Ching* 7132 (US). Kwangtung, China: *W. T. Tsang* 26363 (A).

Pamphilia aurea Martius. Brazil: *H. S. Irwin, H. Maxwell, & D. C. Wasshausen* 20974 (US); *Irwin et al.* 29208 (GH). *P. pedicellata* var. *ovalis* Perk. Brazil: *Y. Mexia* 5778 (US). *P. styracifolia* A. DC. Brazil: *J. E. de Oliveira s.n.* (US #2123954).

Parastyrax lacei W. W. Smith. Burma: *J. H. Lace s.n.* (E).

Pterostyrax cavaleriei Chun. Kweichow, China: *Y. Tsiang* 6434 (US). *P. corymbosus* Sieb. & Zucc. Japan: *Y. Tateishi* 7010 (US). *P. hispidus* Sieb. & Zucc. Königl. Botanischer Garten, Breslau, Poland: *C. Baenitz s.n.* (US #1155541).

Rehderodendron indochinense Li. Yunnan, China: *K. M. Feng* 12307 (A). *R. kweichowense* Hu. Kwangsi, China: *S. K. Lau* 28706 (A). *R. macrocarpum* Hu. Szechwan, China: *W. P. Feng* 2663 (A); *T. C. Lee* 2959 (US).

Sinojackia henryi (Dümmer) Merr. Szechwan, China: *A. Henry* 8865 (GH). *S. rehderiana* Hu. Without location: *collector unknown* 10314 (L). *S. xylocarpa* Hu. Kiangsu, China: *W. Cheng* 4494 (US).

Styrax agrestis G. Don. Solomon Islands: *L. J. Brass* 3261 (A). *S. ambiguus* Seub. Brazil: *E. Warming s.n.* (US #1110459). *S. americanus* var. *americanus* Lam. Florida: *F. Rugel s.n.* (US #512620). *S. americanus* Lam. var. *pulverulentus* (Michaux) Perk. Escambia Co., Alabama: *E. S. Ford* 5242 (US). Hardin Co., Texas: *V. L. Cory* 52817 (US). *S. argenteus* var. *argenteus* Presl. Nayarit, Mexico: *J. G. Ortega* 60 (US). *S. argenteus* Presl var. *hintonii* (Bullock) Gonsoulin. Michoacán, Mexico: *Bro. G. Arsène* 8472 (US). *S. argenteus* Presl var. *ramirezii* (Greenman) Gonsoulin. Chiapas, Mexico: *C. A. Purpus* 157 (US). *S. benzoin* Dryander. Java, Indonesia: *Blume s.n.* (A). Trinidad, West Indies: *W. E. Broadway s.n.* (US #1194642). *S. camporum* Pohl. Brazil: *G. Hatschbach & O. Guimaraes* 21776 (US); *L. O. Williams* 6432 (GH). *S. cespedesii* Perk. Colombia: *E. L. Little, Jr.* 8820 (US). *S. conterminus* Smith. El Salvador: *P. H. Allen* 7184 (US). *S. crotonoides* Clarke. Singapore: *Field* 36937 (A). *S. davillifolius* Perk. Venezuela: *A. Jahn s.n.* (US #1189096). *S. faberi* Perk. China: *C. O. Levine* 467 (GH). *S. fanshawei* Sandwith. British Guiana: *D. B. Fanshawe* 5607 (US). *S. ferrugineus* Nees & Martius. Brazil: *Irwin et al.* 13659 (US); *G. O. A. Malme* 1958a (GH). *S. formosanus* Matsumura. Formosa: *Wilson* 10266 (A). *S. glaber* Swartz. St. Kitts, West Indies: *R. K. Wadsworth* 495 (A). *S. glabratus* Schott. Brazil: *A. Loeffgren* 4165 (US). *S. glabrescens* var. *glabrescens* Benth. Mexico: *Purpus* 88 (US). *S. glabrescens* Benth. var. *pilosus* Perk. Mexico: *E. Matuda* 4179 (US). *S. grandifolius* Aiton. Garland Co., Arkansas: *C. F. Adams s.n.* (US #2420427). Gwinnett Co., Georgia: *H. A. Allard* 194 (US). *S. henryi* Perk. Formosa: *Wilson* 9933 (A). *S. heteroclitus* Macbride. Juanjui, Peru: *G. Klug* 4282 (US). *S. hypargyreus* Perk. Venezuela: *H. Pittier* 15725

(US). *S. hypoglaucus* Perk. Kwangsi, China: *Tsang 24105* (A). *S. jaliscanus* S. Watson. Mexico: *C. A. Pringle 11012* (US). *S. japonicus* Sieb. & Zucc. Japan: *N. Fukuoka 5852* (US); *M. Hiroe 10251* (A). Washington, D. C.: *G. B. Sudworth s.n.* (US #478713). *S. langkongensis* W. W. Smith. Yunnan, China: *Rock 10546* (A). *S. latifolius* Pohl. Brazil: *collector unknown 7269* (US); *H. M. Curran 627* (GH). *S. longifolius* Standley. Peru: *R. Ferreyra 4546* (US). *S. macrocalyx* Perk. Colombia: *J. C. Mutis 2465* (US). *S. macrotrichus* Perk. Colombia: *Mutis 5207* (US). *S. martii* Seub. Brazil: *Irwin et al. 32264* (US). *S. micrasterus* Perk. Colombia: *Mutis 4260* (US). *S. microphyllus* Perk. Colombia: *Mutis 2558* (US). *S. obtusifolius* Griseb. Cuba: *R. A. Howard 5618* (US); *A. Gonzales 477* (A). *S. ochraceus* Urban. West Indies: *E. L. Ekman 13883* (US); *Bro. A. H. Liogier 11364* (GH). *S. officinalis* L. var. *fulvescens* (Eastw.) Munz & Johnston. California: *L. P. Abrams 6273* (US); *E. A. Purer 6680* (US). *S. officinalis* L. var. *redivivus* (Torrey) Howard. Placer Co., California: *E. Crum 2043* (US). *S. ovatus* A. DC. Peru: *Mexia 8171* (GH). *S. pallidus* A. DC. Venezuela: *L. Williams 10353* (A). *S. paralleloneurus* Perk. Sumatra, Indonesia: *H. O. Forbes 2354* (GH). *S. pearcei* Perk. Bolivia: *O. Buchtien 5953* (US). *Styrax pentlandianus* Remy. Bolivia: *A. Miguel 2867* (US). *S. philadelphoides* Perk. Chekiang, China: *H. H. Hu 1689* (A). Kiangsu, China: *L. F. Tsu s.n.* (US #1346056). *S. plataniifolius* Engelmann. Kendall Co., Texas: *E. J. Parker 11474* (US). *S. pohlii* A. DC. Brazil: *collector unknown 2885* (US). *S. poissonianus* Perk. Peru: *C. Schunke A39* (US). *S. portoricensis* Krug & Urban. West Indies: *collector unknown s.n.* (US #404089). *S. pseudargyrophyllus* Sleumer. Colombia: *L. Muñoz s.n.* (US #1950764). *S. serrulatus* Roxb. Tibet: *G. H. Cave 1.9.1920* (A). *S. subcordatus* Moric. Brazil: *Irwin et al. 12490a* (GH). *S. subcrenatus* Handel-Mazz. Hainan, China: *F. C. How 71118* (A). *S. suberifolius* Hooker & Arnott. Kwangtung, China: *Tsang 25927* (A). Hong Kong: *W. Y. Chun 5071* (A). Taiwan: *A. Hsieh s.n.* (US #2063471). *S. sumatranus* J. J. Smith. Sumatra, Indonesia: *Yates 2532* (A). *S. yapobodensis* (Idrobo & R. E. Schultes) Steyerl. Colombia: *R. E. Schultes 14394* (A).

EXPLANATION OF PLATES

PLATE I

Transverse sections of petiole and midrib illustrating patterns of vascularization. A, *Afrostryax kamerunensis* (Zenker 3922): 1, medial petiole; 2, distal petiole; 3, midrib 2 mm. from petiole; 4, midrib 4 mm. from petiole; 5, medial midrib. B, *Lissocarpa guianensis* (de la Cruz 3076): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. Key to tissues: solid black, sclerenchyma; stipple, phloem; vertical lines, xylem.

PLATE II

Transverse sections of petiole and midrib illustrating patterns of vascularization. A, *Parastyrax lacei* (Lace s.n.): 1, medial petiole; 2, distal petiole; 3, midrib 5 mm. from petiole; 4, medial central actinodromous vein. B, *Rehderodendron kweichowense* (Lau 28706): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. Key to tissues: solid black, sclerenchyma; stipple, phloem; vertical lines, xylem.

PLATE III

Transverse sections of petiole and midrib illustrating patterns of vascularization. A, *Pamphilia aurea* (Irwin et al. 29208): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, midrib 2 mm. from petiole; 5, medial midrib. B, *Sinojackia xylocarpa* (Cheng 4494): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. C, *Styrax americanus* (Rugel s.n.): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. D, *Styrax japonicus* (Fukuoka 5852): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. Key to tissues: solid black, sclerenchyma; stipple, phloem; vertical lines, xylem.

PLATE IV

Transverse sections of petiole and midrib illustrating patterns of vascularization. A, *Styrax benzoin* (Broadway s.n.): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. B, *Styrax micrasterus* (Mutis 4260): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. C, *Styrax ochraceus* (Ekman 13883): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. D, *Styrax pohlii* (collector unknown 2885): 1, basal petiole; 2, medial petiole; 3, distal petiole; 4, medial midrib. Key to tissues: solid black, sclerenchyma; stipple, phloem; vertical lines, xylem.

PLATE V

Venation patterns (leaves not drawn to scale). A, *Afrostryax kamerunensis* (Zenker 3922). B, *Lissocarpha benthamii* (Gleason 724). C, *Alniphyllum eberhardtii* (Petelot 4490). D, *Alniphyllum pterospermum* (Wilson 9992). E, *Bruinsmia styracoides* (J. & M. S. Clemens 50339). F, *Halesia carolina* (Nesom s.n.). G, *Halesia macgregorii* (Ching 2132). H, *Huodendron tibeticum* (Rock 22020). I, *Melliodendron xylocarpum* (Ching 7132).

PLATE VI

Venation patterns (leaves not drawn to scale). A, *Pamphilia aurea* (Irwin et al. 20974). B, *Parastyrax lacei* (Lace s.n.). C, *Pterostyrax hispidus* (Baenitz s.n.). D, *Rehderodendron indochinense* (K. M. Feng 12307). E, *Sinojackia xylocarpa* (Cheng 4494). F, *Styrax agrestis* (Brass 3261). G, *Styrax argenteus* var. *argenteus* (Ortega 60). H, *Styrax faberi* (Levine 467). I, *Styrax officinalis* var. *redivivus* (Crum 2043).

PLATE VII

Leaf areolation. A, *Afrostryax kamerunensis* (J. Mildbraed 10688), $\times 107$, well-developed areoles. B, *Huodendron biaristatum* (Petelot 6339), $\times 40$, observe relatively consistent size and shape of areoles. C, *Sinojackia xylocarpa* (Cheng 4494), $\times 27$, relatively well-developed areoles. D, *Styrax glabratus* (Loefgren 4165), $\times 36$, imperfectly developed areoles. E, *Styrax japonicus* (Fukuoka 5852), $\times 27$, incompletely developed areoles. F, *Styrax suberifolius* (Chun 5071), $\times 27$, observe branching of ultimate veinlets and imperfectly developed areoles.

PLATE VIII

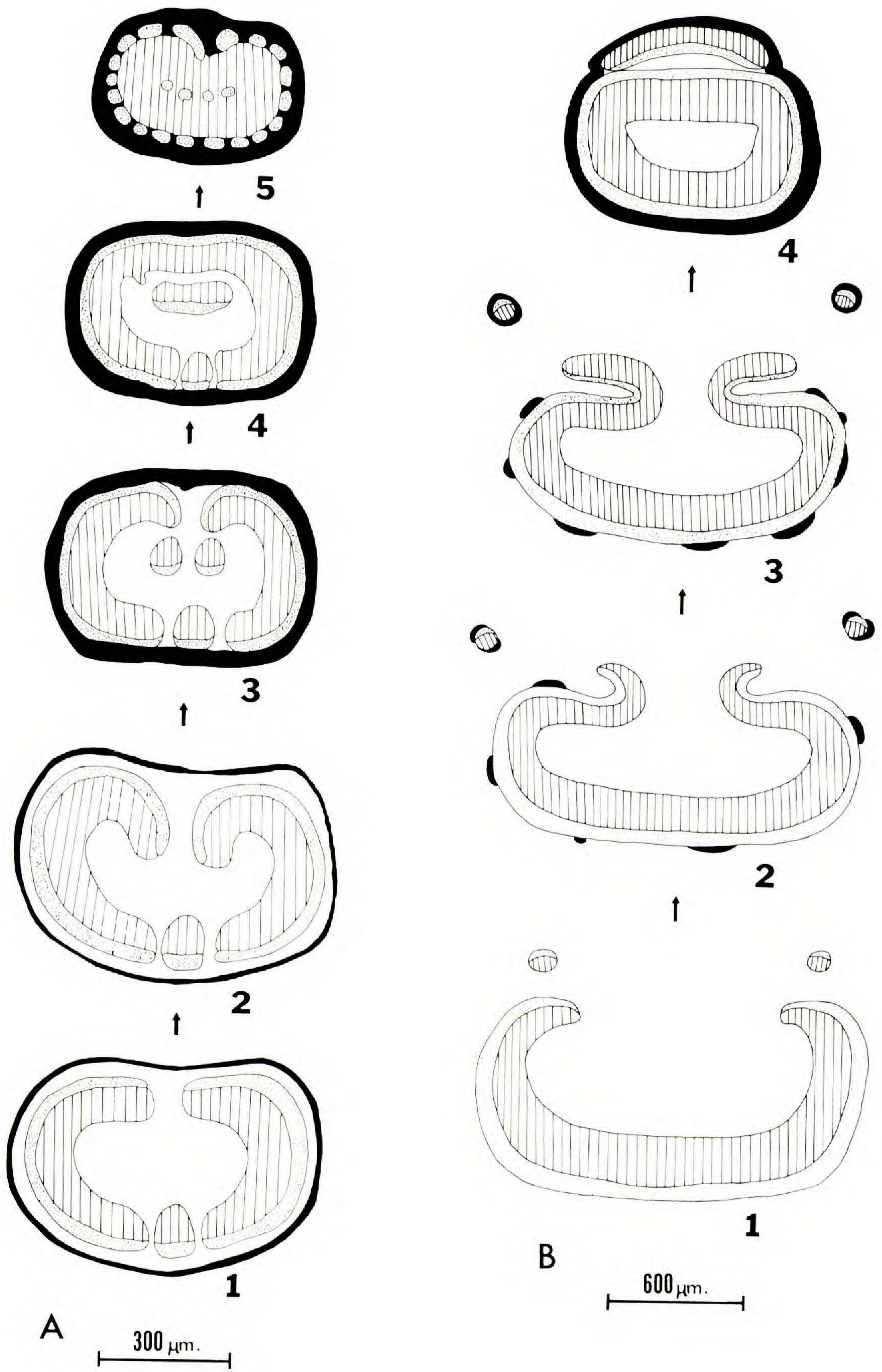
Tooth morphology. A, B, *Styrax serrulatus* (Cave 1.9.1920): A, $\times 40$, note vascularization of tooth by tertiary vein. B, $\times 107$, observe expansion of vascular tissue at base of tooth. C, *Styrax japonicus* (Fukuoka 5852), $\times 40$, glandlike cap on apex of tooth. D, *Styrax faberi* (Levine 467), $\times 107$, note tapering of vascular tissue at apex of tooth below glandlike cap.

PLATE IX

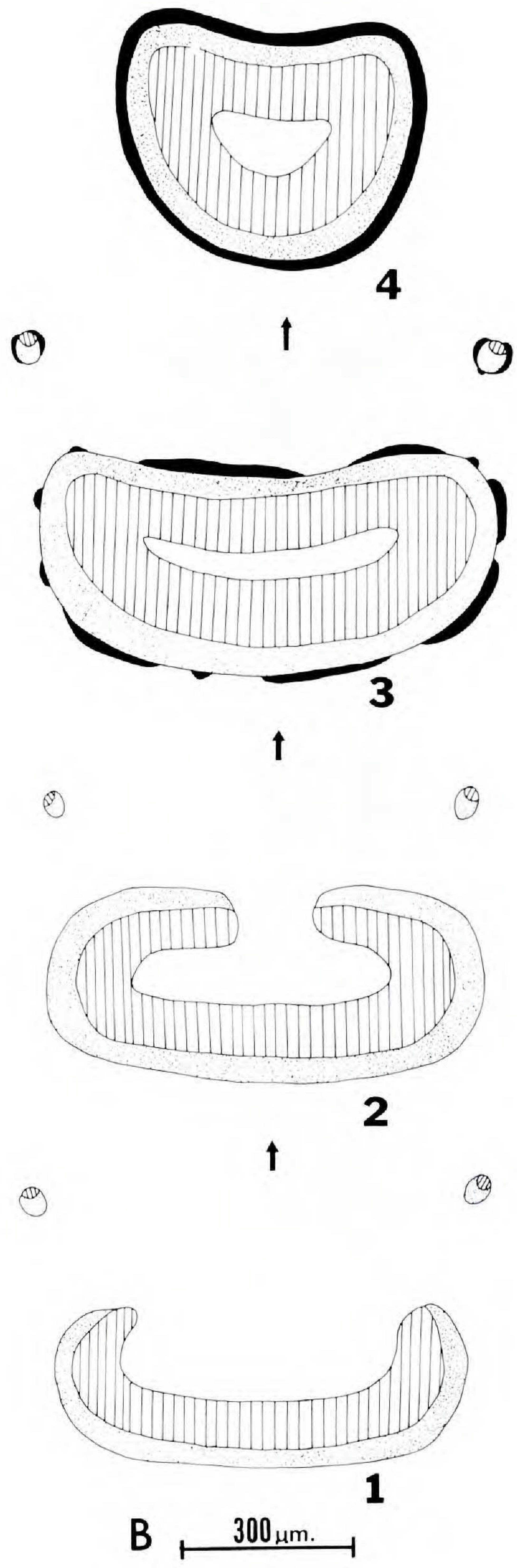
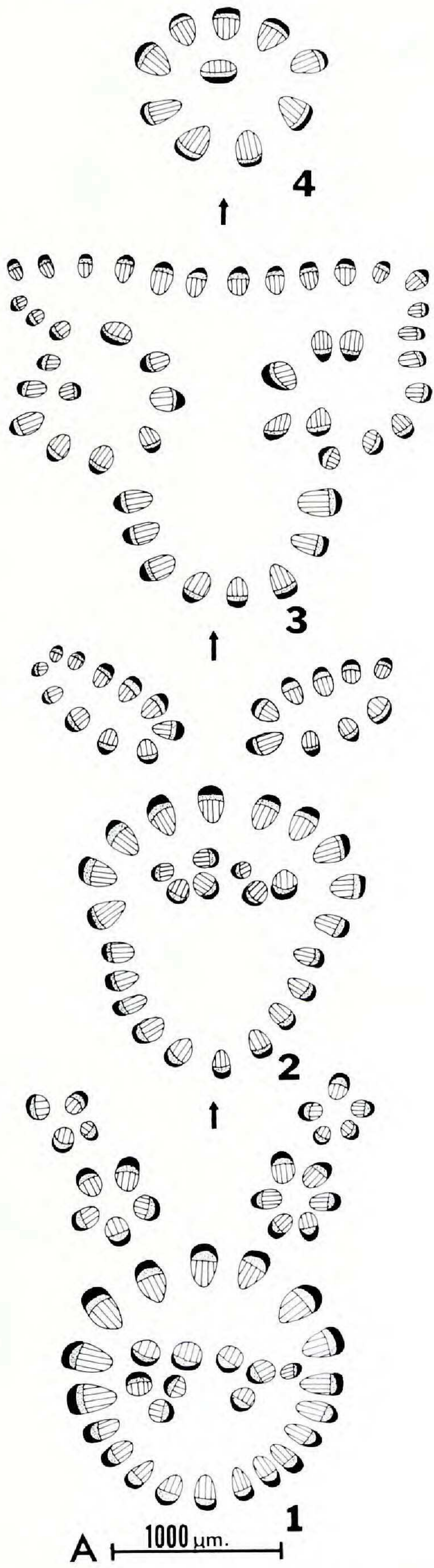
Transverse sections of lamina. A, *Afrostryax lepidophyllus* (Gilbert 10222), $\times 400$, note prominent papillate abaxial epidermis. B, *Bruinsmia styracoides* (Clemens 2970), $\times 160$, observe isodiametric shape of spongy parenchyma cells. C, *Huodendron chunianum* (Tsai 60571), $\times 160$, prominent cuticular striations on both surfaces. D, *Pamphilia aurea* (Irwin et al. 29208), $\times 107$, note upright cells in adaxial sheath extension. E, *Styrax ferrugineus* (Irwin et al. 13659), $\times 160$, observe prominent adaxial bundle sheath extension. F, *Styrax glaber* (Wadsworth 495), $\times 160$, note absence of bundle sheath extension.

PLATE X

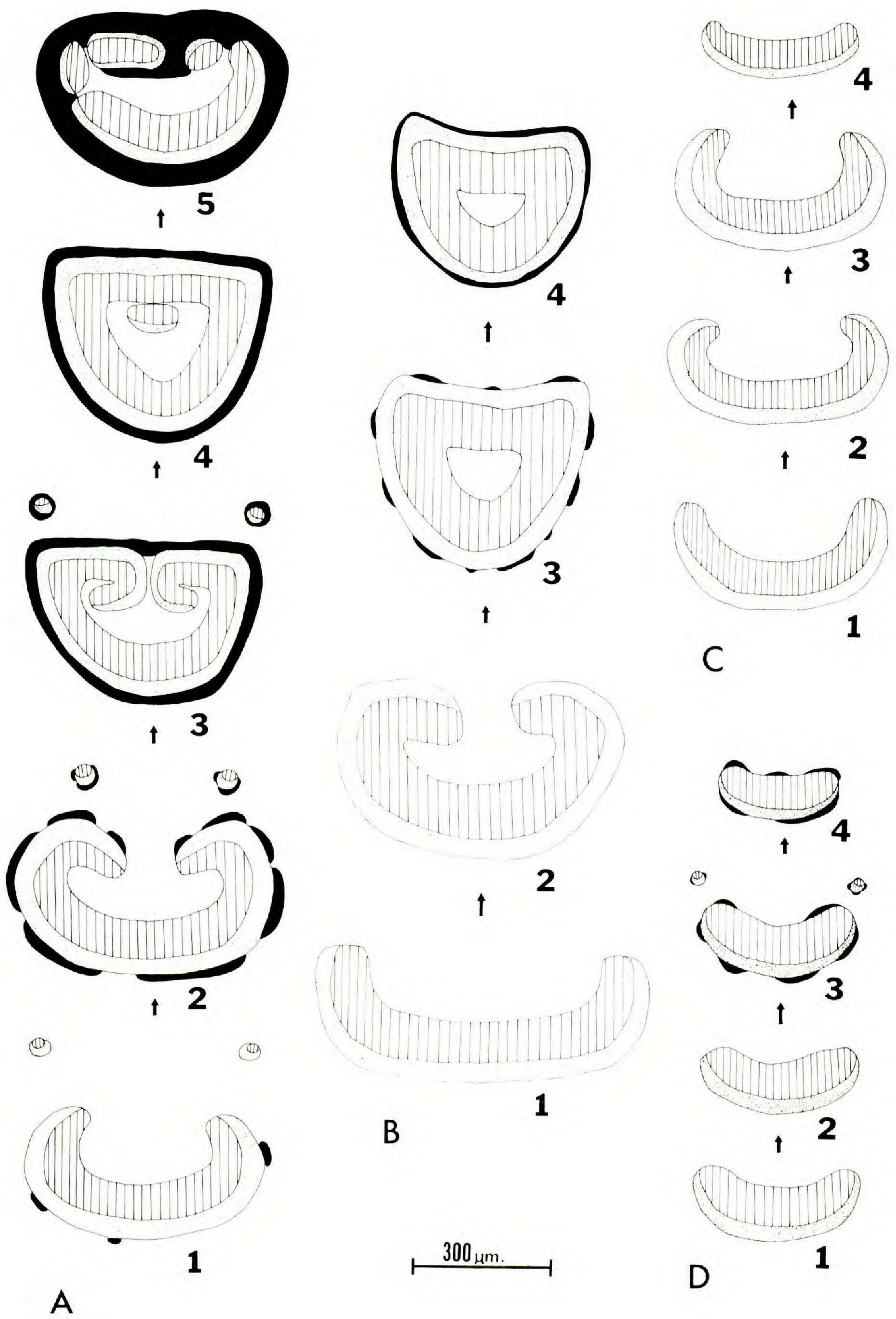
Transverse sections of lamina. A, *Styrax macrotrichus* (Mutis 5207), $\times 265$, observe weakly differentiated mesophyll. B, *Styrax micrasterus* (Mutis 4260), $\times 160$, note compact spongy parenchyma. C, *Styrax ochraceus* (Ekman 13883), $\times 135$, observe three layers of palisade parenchyma. D, *Styrax philadelphoides* (Tsu s.n.), $\times 160$, bundle sheath extensions occurring in both adaxial and abaxial positions. E, *Styrax portoricensis* (us #404089), $\times 265$, observe weakly differentiated mesophyll. F, *Styrax pseudargyrophyllus* (Muñoz s.n.) $\times 160$, note biseriate epidermis (hypodermis?).

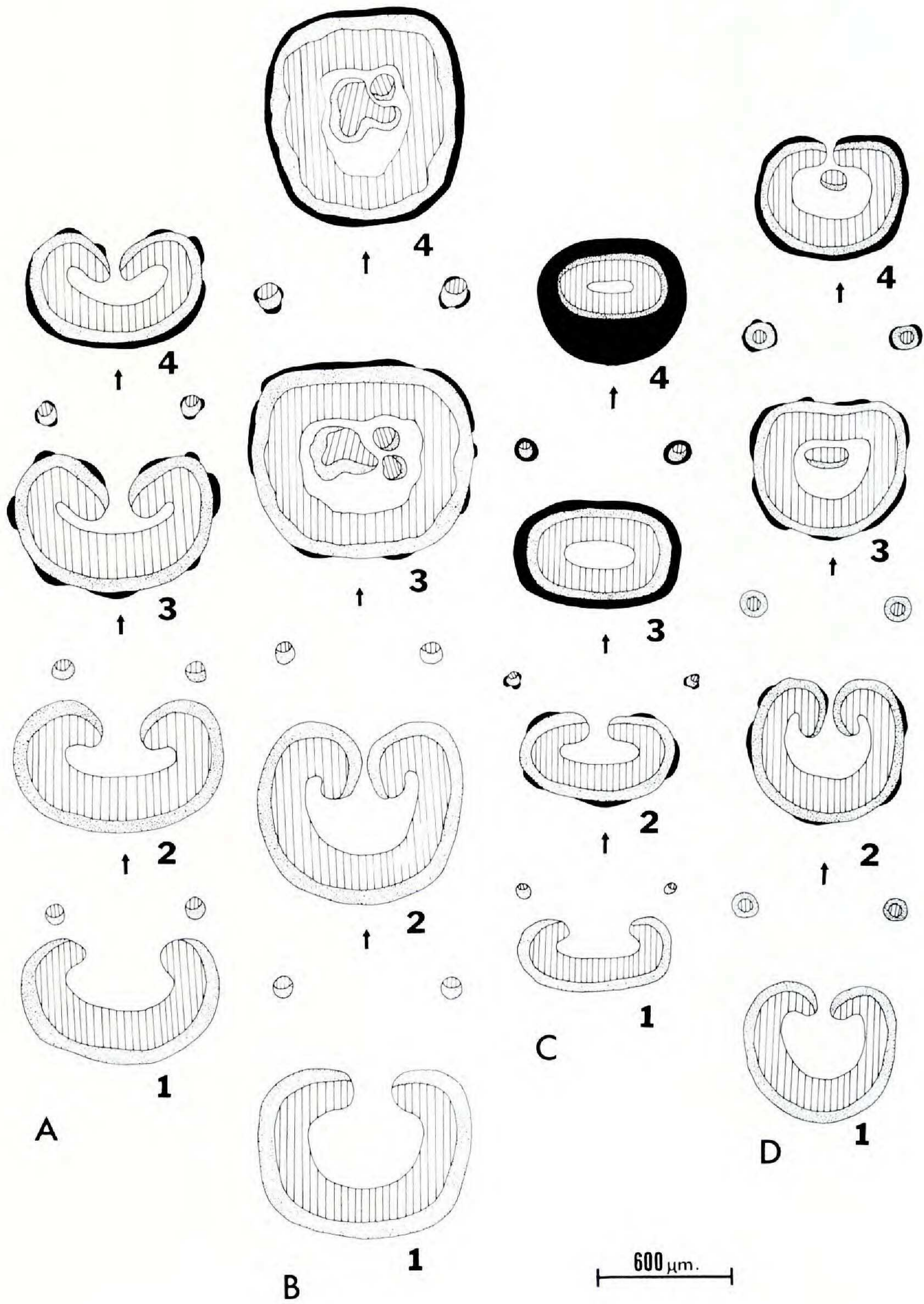


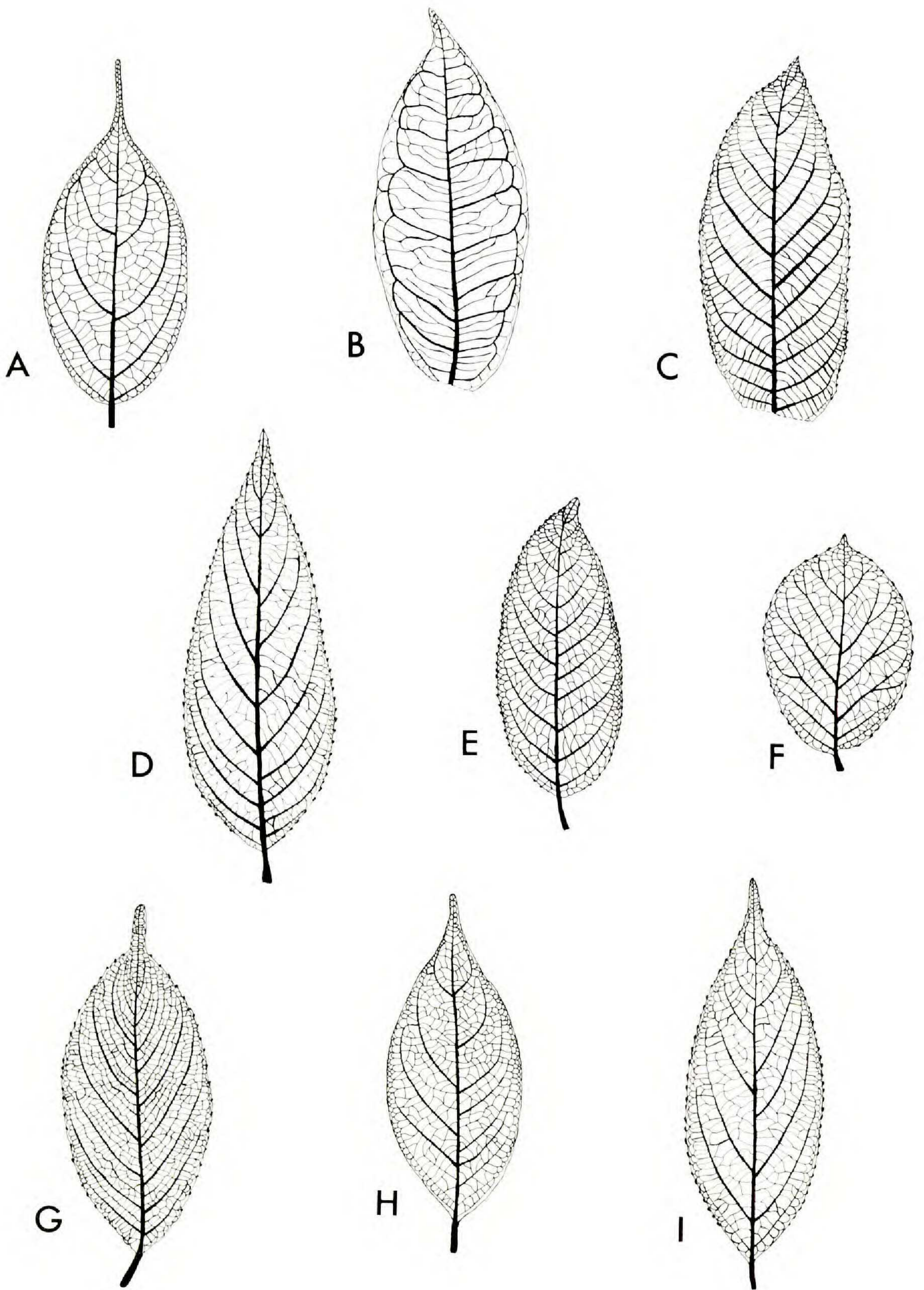
SCHADEL & DICKISON, LEAF ANATOMY



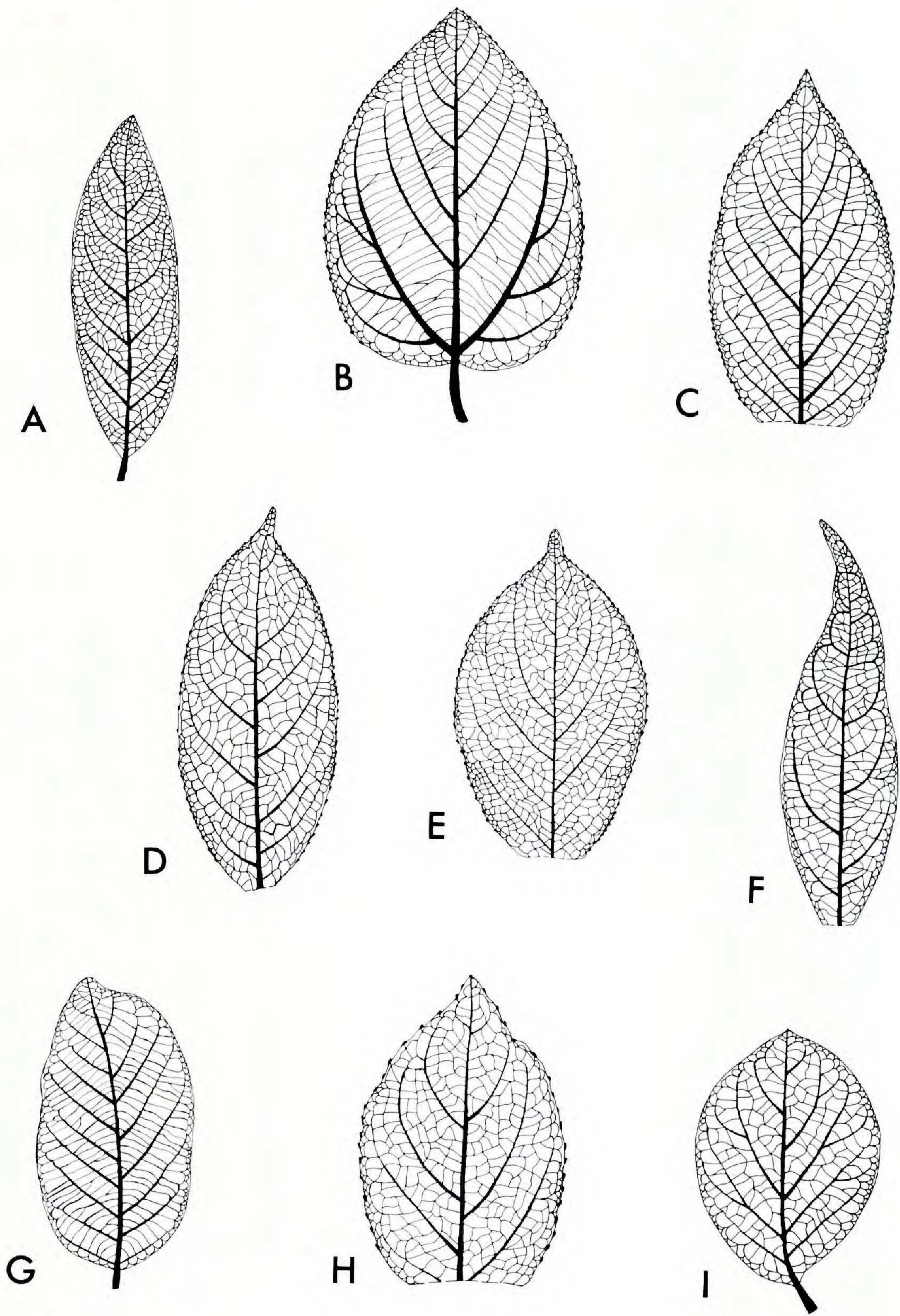
SCHADEL & DICKISON, LEAF ANATOMY

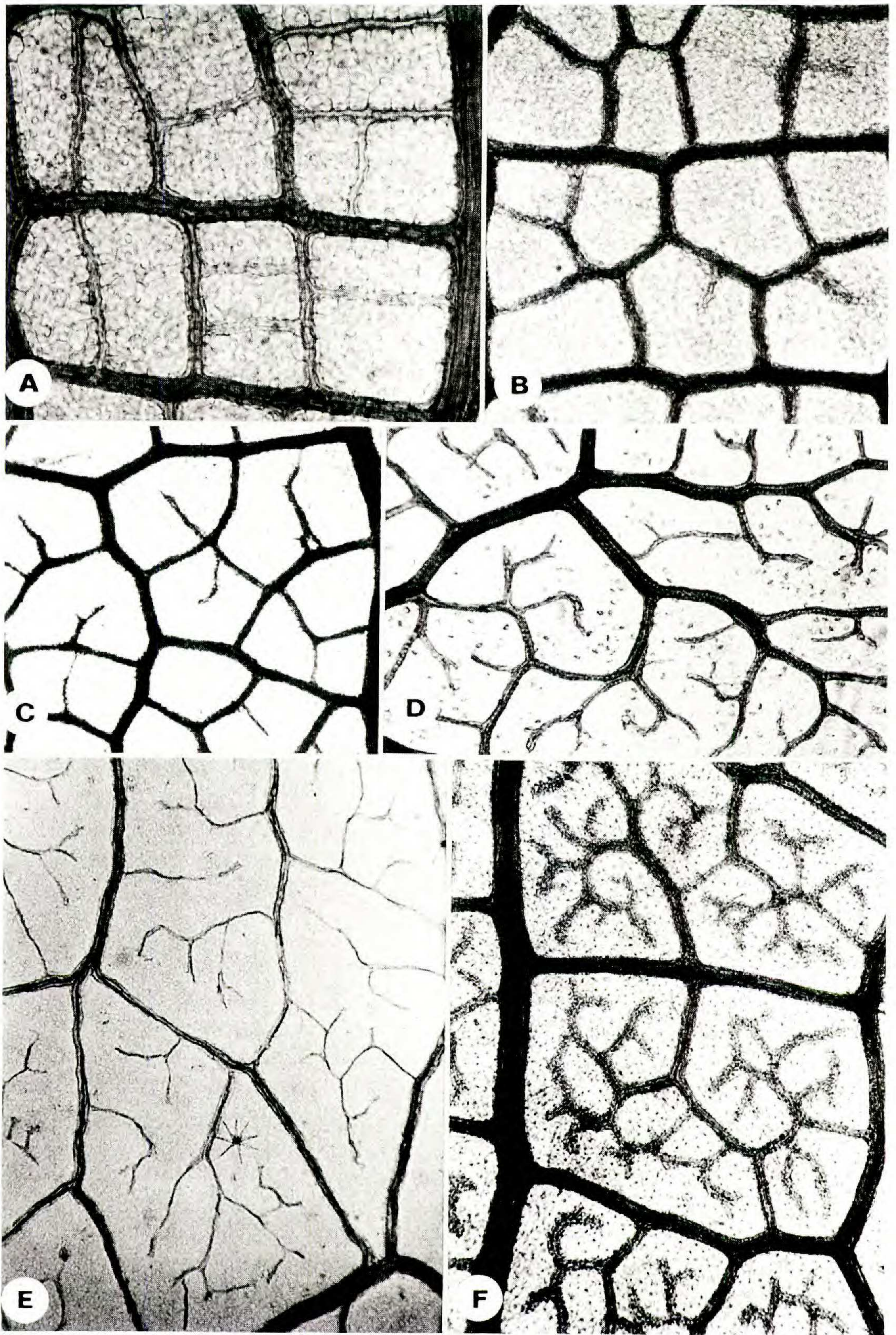




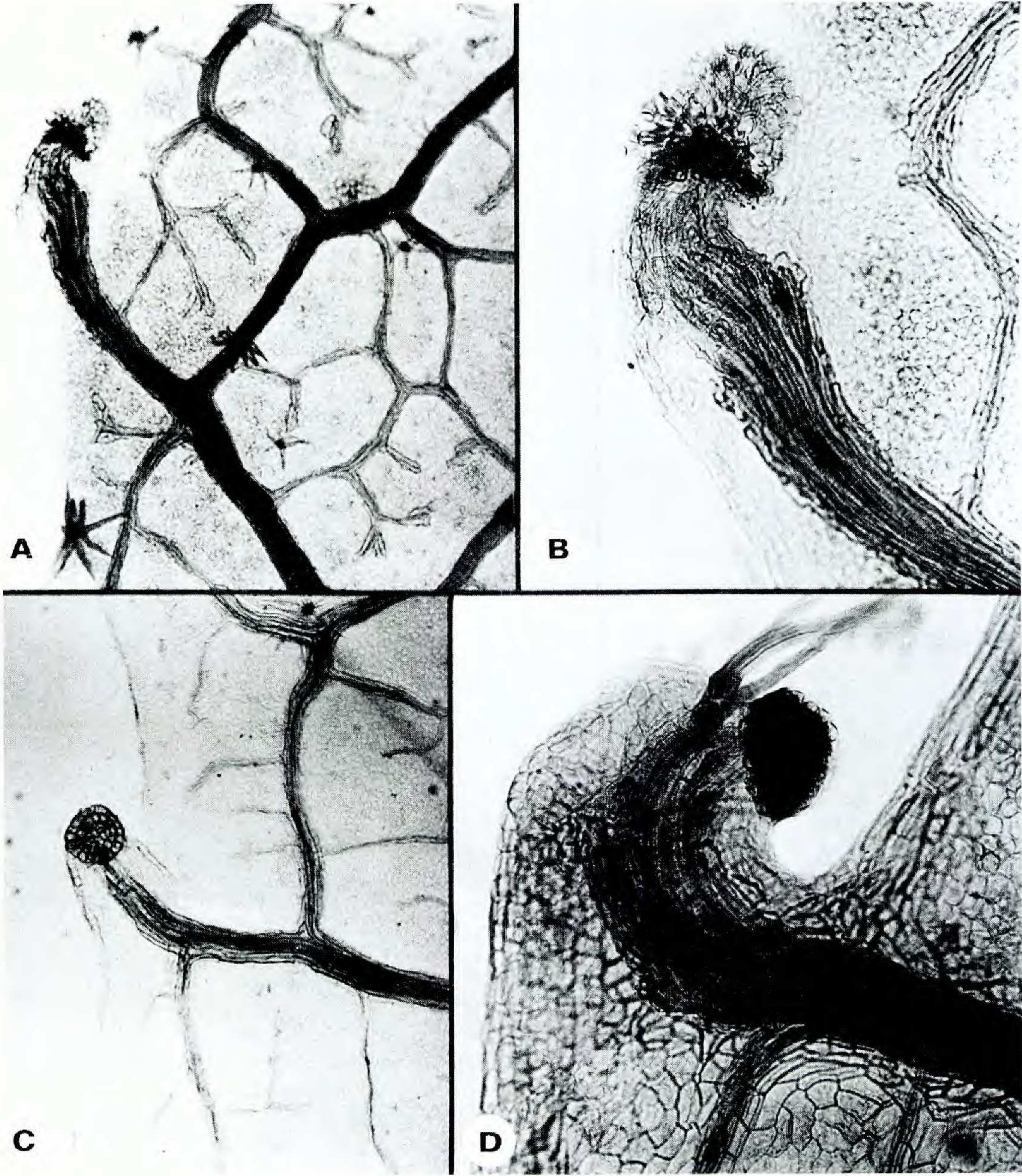


SCHADEL & DICKISON, LEAF ANATOMY





SCHADEL & DICKISON, LEAF ANATOMY



SCHADEL & DICKISON, LEAF ANATOMY

